

4.2.4 Disturbance and Vascular Plants

Crusts can affect vascular plant germination, survival, and nutrition. Lichen-moss crusts in areas with frost heaving (as in cool deserts) increase perennial vascular plant seed entrapment, germination, establishment, survival, biomass, and nutritional status (Belnap and Harper 1995). In these deserts, disturbance that flattens frost-heaved surfaces and/or eliminates mosses and lichens can have a negative effect on some or all of these characteristics. However, germination and survival of some exotic annual grasses can be enhanced with biological crust disturbance.

In hot deserts, seed entrapment, biomass, and fecundity of annual plants is generally increased when smooth cyanobacterial crusts are disturbed (Prasse 1999), although there are some exceptions (Guterman 1994). Disturbance of smooth cyanobacterial crusts enhances germination of some annual species, while decreasing germination of others (Zaady et al. 1997). Rugose crusts in hot deserts have received little study, and no work has addressed the effects of disturbance on seed entrapment. Effects on germination in rugose crusts appear to be species dependent. In contrast to smooth crusts, disturbance to hot desert rugose crusts lessens survival and biomass of perennial plants (McIlvanie 1942; Crisp 1975).

Biological soil crusts have been shown to influence availability of many plant-essential nutrients. Crust loss can result in less plant-available magnesium, potassium, iron, calcium, phosphorus, manganese, and sulfur (Harper and Belnap in press). The spatial distribution of nutrients is also affected by disturbance, as disturbance will alter the relative distribution of biological crust components (i.e., lichens, mosses, cyanobacteria) across the landscape (Klopatek 1992).

4.2.5 Disturbance and Surface Albedo

Trampling of dark-crusts exposes underlying, lighter soils, thus increasing albedo (reflectance) by up to 50% at most wavelengths measured (Fig. 3.1). This increased albedo represents an energy loss from the soil surface of approximately 40 watts/m² and can reduce soil temperatures by up to 14°C (Belnap 1995). Such changes in reflectance are especially apparent using satellite imagery, as can be seen in the Negev Desert, along the U.S.-Mexico border, and in Australia. Much of this difference is attributed to loss of biological soil crusts (Graetz and Tongway 1986). Large-scale changes in surface albedo may contribute to changes in regional climate patterns (Sagan et al. 1979).

4.2.6 Disturbance and Soil Hydrology

The effect of biological soil crust disturbance on soil hydrology is very site specific. Water infiltration, runoff, and resultant soil moisture are influenced by soil surface roughness, soil texture, microtopography, surface albedo and temperature, vegetative cover (both vascular and non-vascular), and climatic conditions. All these factors can be altered when biological crusts are disturbed. In general, disturbance flattens pinnacled and rolling crusts, thus decreasing water infiltration and increasing runoff (Fig. 3.3). In hot deserts, disturbance to smooth and rugose lichen- or cyanobacterial-crustured surfaces can increase overall infiltration rates (Greene et al. 1990; Eldridge et al. 2000). However, this increase in infiltration may negatively affect nearby vascular plants that depend on interspace runoff for survival (see Section 3.6). Soil structure alteration as a result of soil compaction can also reduce infiltration rates. Available soil moisture results from a complex interaction of many soil and plant characteristics, including infiltration, soil moisture-holding capacity, albedo, plant root density, etc. Only two studies have addressed the combined effects of crusts on available soil moisture, with disparate results. One study found increased soil moisture under intact crusts, while the other found soil moisture increased under disturbed crusts (reviewed in Harper and Marble 1988).

4.2.7 Disturbance Relative to Water and Wind Erosion

Compressional disturbance damages soil-stabilizing cyanobacterial sheath material both at and below the soil surface. The damage below the surface is irreparable, as living cyanobacteria are not present to regenerate sheath material. As greater than 75% of photosynthetic biomass and productivity is from organisms living in the top 3 mm of soils, disturbance that results in even small soil losses can dramatically reduce site fertility and further reduce soil surface stability (Garcia-Pichel and Belnap 1996).

4.2.7.1 Water Erosion: Globally, all studies show crust cover loss significantly increases water erosion of both coarse- and fine-textured soils. Continuous tracks have a greater impact than non-connected disturbances (such as hoof prints) because of increased water flow volume and velocity along the tracks (Webb and Wilshire 1983). Crushing of cyanobacterial connections between particles results in smaller, isolated soil aggregates that are then more easily moved by water. In addition, surfaces flattened by compressional disturbances are less able to reduce water velocity, thereby allowing

movement of larger soil particles and reducing opportunities for sediment to settle out.

4.2.7.2 Wind Erosion: All studies of wind erosion indicate that disturbed soils are more susceptible to wind erosion than undisturbed soils when dry (Fig. 4.6). When crusts are crushed or absent, soil particle movement is initiated at lower wind speeds, as resistance to wind erosion increases with better soil crust development. Well-developed crusts (with lichens and mosses) on both silt and sandy soils have 2 to 130 times greater resistance to soil erosion than less well-developed crusts or bare soil (Fig. 4.7; Williams et al. 1995b; McKenna-Neuman 1996; Belnap and Gillette 1997, 1998; Leys and Eldridge 1998). Vehicle tires result in greater damage than hooves on a given soil type (Belnap and Gillette 1998).

Decreased resistance of soils to wind erosion is directly associated with increased sediment movement. All experimental disturbances applied to crusts show increased sediment production—up to 35 times that of adjacent undisturbed crusts (Leys and Eldridge 1998; Williams et al. 1995b). Nearby soil crusts are often buried by blowing sediment, resulting in death of photosynthetic organisms.

4.3 Factors Influencing Natural Recovery Rates

Recovery rates are dependent on many factors, including disturbance type, severity, and extent; vascular plant community structure; adjoining substrate condition; inoculation material availability; and climate during and after disturbance. Comparing recovery rates reported in the literature is highly problematic, as studies range over a wide array of climatic zones, soil types, and levels of disturbance, and these factors are seldom quantified. Thus, most studies can only be used to define the general range of recovery rates. Some studies do report climate, soil, and/or disturbance data such that comparisons are possible (Anderson et al. 1982a; Jeffries and Klopatek 1987; Callison et al. 1985; Cole 1990; Belnap 1995, 1996; Eldridge 1996; Belnap and Warren 1998).

Examination of these studies indicates that general recovery times can be predicted for soil crusts in different environments. Most recovery time calculations for crust cover assume a linear recovery rate. On the Colorado Plateau, scalped plots were reassessed 2 to 5 and 10 to 14 years after disturbance. After 2 to 5 years, cyanobacterial cover was predicted to recover in 45 to 110 years, whereas it recovered within 14 to 34 years. Thus, linear assumptions greatly overestimated recovery time. Lack of moss recovery prevented useful estimates at two of the three sites at the earlier sampling time. At one site, early estimates were 400 years to recovery, while later estimates were 42

Figure 4.6 Resistance of sandy loam soils to wind erosion following disturbance to a well-developed biological soil crust in four time classes. Threshold friction velocity is the force required to detach soil particles from the surface. Time classes indicate the length of time since disturbance to the control. Following determination of threshold friction velocities for controls, treatments were applied as follows: Foot = one pass wearing lug-soled boots; Tire, 1 Pass = one pass of a four-wheel drive vehicle with knobbed tires; Tire, 2 Pass = two passes of a four-wheel drive vehicle with knobbed tires. Within each time sequence, controls were significantly more resistant to wind erosion than treated surfaces. Adapted from Belnap and Gillette (1997).

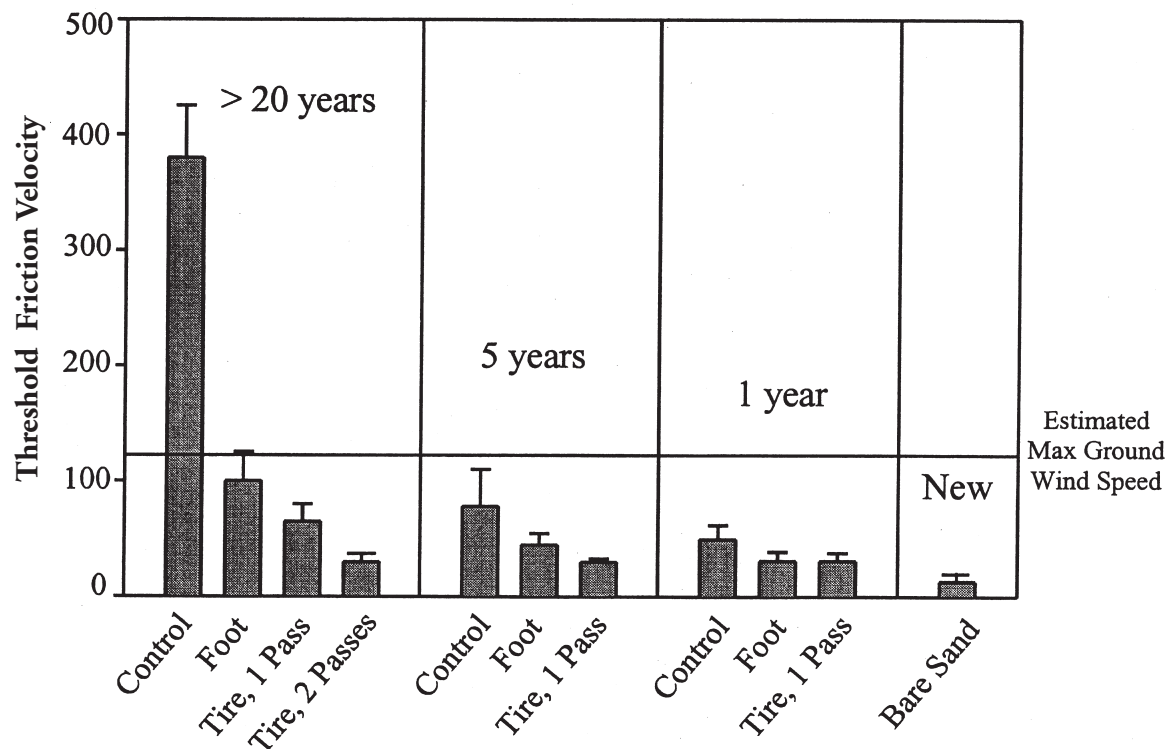
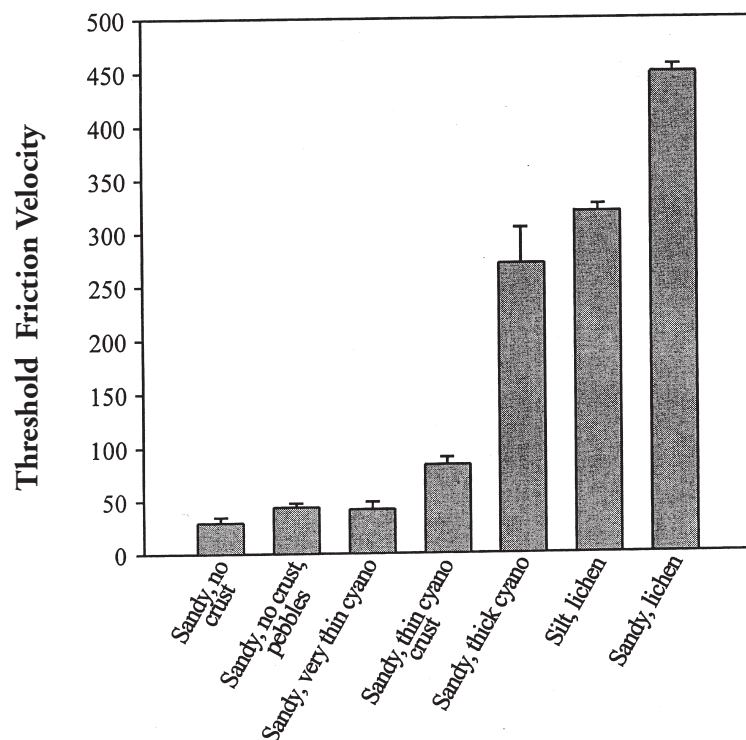


Figure 4.7 Resistance of soil surfaces to wind erosion. Resistance increases with surface protection and development of the biological soil crust. The greatest amount of resistance is demonstrated by soils with well-developed biological crusts characterized by a diverse lichen flora. Adapted from Belnap and Gillette (1998).



years. As with cyanobacteria, linear extrapolations overestimated recovery time. In contrast, *Collema* recovery after 3 years was estimated at 85 years; after 14 years, the estimate for full recovery was 50 years, a fairly close match. *Collema* recovery at a second site was highly variable: after 2 years, recovery time was estimated at 487 years; after 11 years, estimates were site dependent, ranging from 40 to 766 years. Original estimates were therefore both under and over estimated, depending on individual site characteristics. Sites with more shade and less sandy soils were quicker to recover than original estimates predicted, while more exposed sites with sandier soils were less able to recover than originally estimated (Belnap, unpublished data).

4.3.1 Sequence of Species Appearance

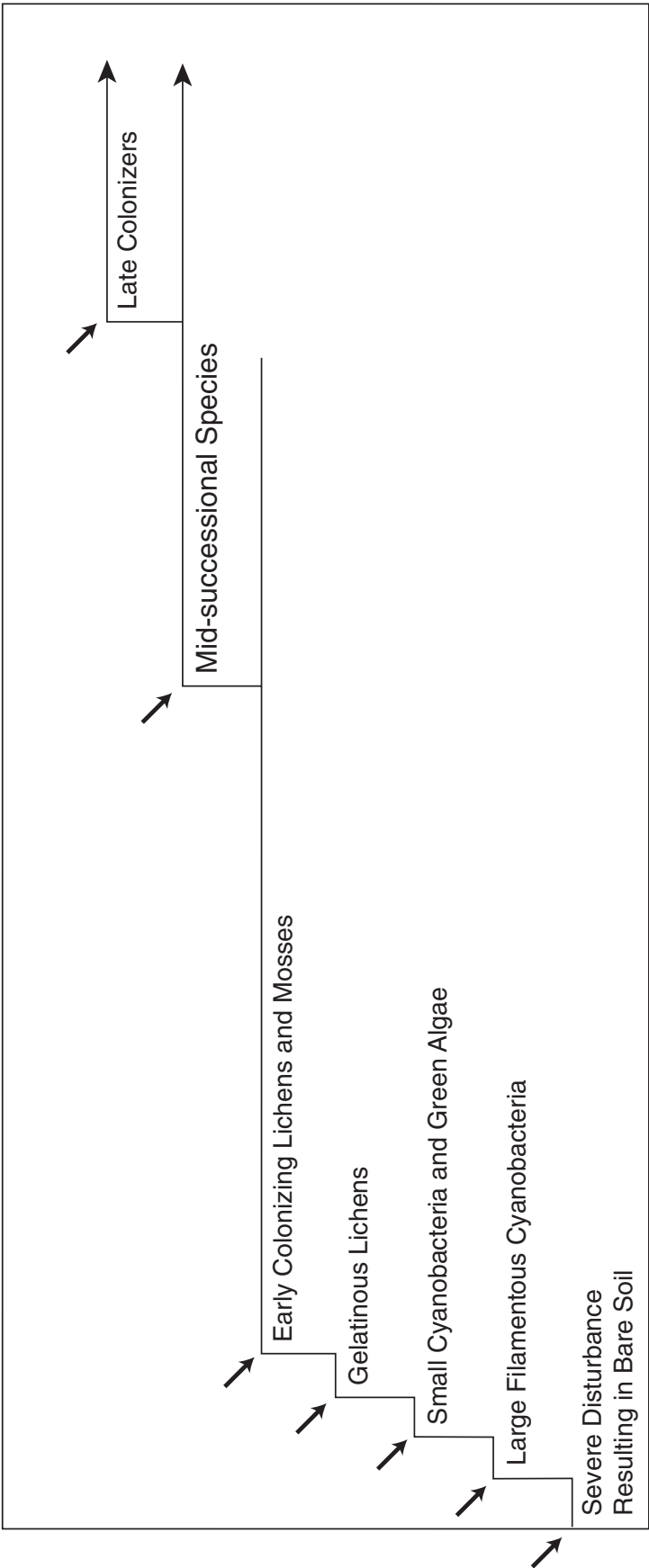
Cyanobacteria and green algae are generally the first photosynthetic species to appear on disturbed soils, probably because of their mobility across soil surfaces and their ability to colonize from the air (Schlichting 1969). Large filamentous cyanobacteria such as *Microcoleus* generally appear first (Fig. 4.3, 4.8), especially on unstable sandy soils (Ashley and Rushforth 1984; Belnap 1995). This species is then followed by smaller cyanobacteria and green algae. Occasionally, desert soils are slightly acidic, and here green algae can be the first to appear (Johansen 1993).

Lichens and mosses require stable soil surfaces for growth. This can be provided by a physical crust or by large, filamentous cyanobacteria. Once soils are stabilized, gelatinous nitrogen-fixing lichens (e.g., *Collema* spp.) are generally the first lichens to appear in disturbed areas, followed by other early-successional lichens and mosses (Table 4.3; Johansen et al. 1984; Belnap 1993). Early-colonizing lichens often disperse phytobiont-containing tissue (e.g., isidia, soredia, or algal-covered spores), as opposed to bare spores, thus precluding the need to find phytobionts on-site.

4.3.2 Soil Texture

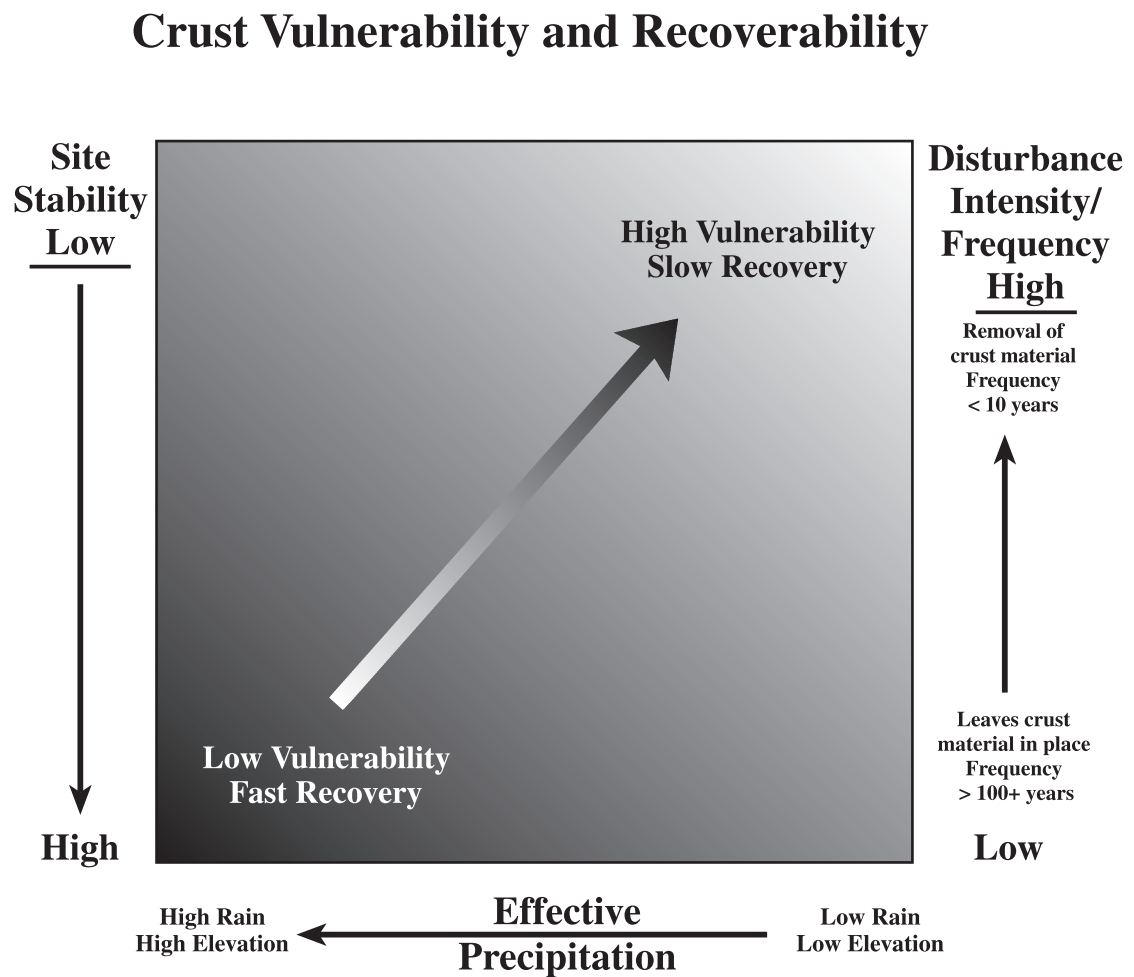
Soil texture influences crust recovery rates. Recovery of all crust components is faster in fine-textured soils than in coarse-textured soils, as fine-textured soils are often stabilized by chemical and rain crusts and retain soil surface moisture longer (Fig. 4.9; as reviewed in Harper and Marble 1988; Johansen 1993; Ladyman and Muldavin 1996). Recovery of the site's wind resistance is also more rapid in fine-textured soils, probably due to crust formation after rainfall. While silty and sandy soils show a similar reduction in wind resistance to vehicle disturbance (83% and 74%, respectively), silty soils show a 50% recovery of wind resistance after a single large rain

Figure 4.8 Generalized recovery sequence for biological soil crusts. Successional stages are illustrated as steps on the diagram. Disturbance input (indicated by arrows) will cause the crust to revert to an earlier successional state, with severe disturbance resulting in complete destruction of the crust. Recovery time is dependent on environmental conditions, including effective precipitation (see Chapter 2). Note that recovery times for mid- and late-successional species in areas with lower effective precipitation are unknown, as recovery times are so long no estimates are possible.



Geographic Region (elevation, average annual precipitation)	Estimated Years to Recovery			
	Gelatinous Lichens	Early Colonizers	Mid Successional	Late Successional
Lower Mojave (<1500 m, 100 mm)	1,200	→ 3,800	unknown	unknown
High Mojave (1500 m, 200 mm)	200	→ 800	unknown	unknown
Colorado Plateau (1500 m, 200 mm)	50	→ 500	unknown	unknown
Northern Great Basin (1000 m, 350 mm)	20	→ 25	→ 60	→ 125

Figure 4.9 *Biological soil crust vulnerability and recoverability based on site stability, effective precipitation, and disturbance regime. Vulnerability decreases and recovery rates increase with increased site stability and effective precipitation, and infrequent disturbance.*



Factors Determining Site Stability		
	Low Stability	High Stability
Soil Texture	Coarse	Fine
Rock/Gravel Cover	Unstable	Stable
Soil Depth	Deep	Shallow
Plant Spacing	Sparse	Dense

Table 4.3 *Characteristics of early-colonizing lichens.*

NOTES

Species	Phytobiont	Reproductive Units
<i>Caloplaca tominii</i>	green algae	soredia
<i>Cetraria islandica</i>	green algae	isidia-like cilia
<i>Cladonia chlorophea</i> group	green algae	soredia
<i>Collema</i> spp.	cyanobacteria	isidia
<i>Cornicularia normoerica</i>	cyanobacteria	finger-like lobes
<i>Endocarpon pusillum</i>	cyanobacteria	algal-covered spores
<i>Leprocaulon microscopum</i>	green algae	soredia
<i>Leptogium corniculatum</i>	cyanobacteria	isidia
<i>Peltigera didactyla</i>	cyanobacteria / green algae	isidia
<i>Peltigera rufescens</i>	cyanobacteria	spores, unspecialized thallus fragmentation
<i>Placidium squamulosum</i>	green algae / cyanobacteria	algal-covered spores

event, while very sandy soils can take up to 10 years for similar recovery (Belnap and Gillette 1997; Belnap and Herrick, unpublished data).

4.3.3 *Climate Regimes*

Crustal organisms are metabolically active only when wet; thus, recovery is faster in regions and microsites with greater effective precipitation (Fig. 4.8, 4.9; Johansen et al. 1993; Harper and Marble 1988). Crusts on north and east slopes, as well as at higher elevations, will recover more quickly than crusts on south and west slopes and at lower elevations. However, as discussed in Sections 2.2.1, 2.2.5, and 2.2.6, there are thresholds along ecological gradients where adequate precipitation results in development of a more diverse and dense vascular flora in lieu of the biological crust.

4.3.4 *Disturbance Type, Frequency, Severity, and Size*

No work has addressed recovery rates of lichens or cyanobacteria from air pollution. In general, crusts are highly susceptible to hot fires; thus, recovery will depend on the size and intensity of fires. As noted previously in “Disturbance Effects” (Section 4.2), most compressional disturbances have similar types of impacts. However, severity of mechanical disturbance can vary widely with disturbance type. Thus, on similar soils, vehicle tracks generally have longer recovery times than disturbances that do not churn the soil or make continuous tracks (Wilshire 1983; Belnap 1996).

Repeated disturbance will generally keep crusts at an early-successional stage (e.g., cyanobacteria-dominated) by preventing lichen or moss colonization (Fig. 4.8; Belnap 1996).

Disturbance severity often controls recovery rates. In western North America, site recovery within a given soil and climate type is faster where disturbances are not severe enough to remove crustal material than it is at sites where crusts were removed. When crusts are completely removed, recovery can be excessively slow, especially in areas with low effective precipitation and/or sandy soils (Fig. 4.9; Eldridge 1996). In contrast, crusts crushed in place with vehicles, foot traffic, and horses recover much faster, especially on fine-textured soils.

Because recolonization of disturbed areas occurs mostly from adjacent, less-disturbed areas, the size and shape of disturbance can affect recovery rates. This is especially true for lichens. Desert soil lichens colonize only infrequently through spores; thus, recovery of lichen cover is mostly dependent on material washing or blowing in from adjoining areas (Eldridge and Ferris 1999). The rate of lichen recovery is much slower in areas with higher internal surface areas relative to perimeter area (Belnap, unpublished data).

4.3.5 *Condition of Adjoining Substrate*

In general, crust recovery is slower if soils adjacent to disturbed areas are destabilized. Detached sediment can both bury adjacent crusts, killing many crustal organisms, and/or provide material for sandblasting nearby surfaces, thus increasing wind erosion (Belnap 1995; McKenna-Neumann et al. 1996; Leys and Eldridge 1998).

4.3.6 *Vascular Plant Community Structure*

Crusts recover more quickly under shrub canopies than in adjacent plant interspaces. This is probably due to greater soil moisture and fertility under shrub canopies. In the Mojave Desert lichen recovery (after complete removal 50 years previously) was 36% under shrub canopies, compared with 4% in the shrub interspaces (Belnap and Warren 1998). A similar pattern was seen in plots established on the Colorado Plateau, where lichen recovery was 2 to 3 times faster under shrubs than adjacent interspaces (Belnap, unpublished data).

The growth of biological soil crusts and vascular plants can be an interactive process (Danin et al. 1989). Eldridge and Greene (1994) present a conceptual model in which crust development at sites is strongly linked to restoration of vital soil processes. As primary colonizers of recovering sites, biological soil crusts enhance microsite fertility and provide safe sites for seeds. In turn, established vascular

plants help stabilize soils, provide shade, and reduce wind speeds at the soil surface, providing conditions conducive to further development and diversification of the biological soil crusts (Wood et al. 1982; Danin et al. 1989).

4.3.7 *Nitrogen and Carbon Fixation*

Overall, nitrogen and carbon fixation rates in biological soil crusts are dependent on its species composition, biomass, and physical structure. Thus, recovery is dependent on recovery rates of specific crustal components. Recovery of nitrogen fixation is dependent on recovery rates of cyanobacteria and cyanolichens. Nitrogen fixation in crusts can require anaerobic microzones in the soils, which may be dependent on buildup of cyanobacterial biomass (Belnap 1996). Carbon fixation increases when lichens and mosses colonize (Phillips and Belnap 1998). As recovery is faster with higher available moisture, both nitrogen and carbon fixation rates are expected to recover faster in cool deserts than in hot deserts, other factors being equal.

Lichen cover may not fully recover after disturbance. On the Colorado Plateau, soils previously occupied by cyanolichens were often occupied by mosses after release from grazing (Belnap, unpublished data). As long as cyanolichen recovery does not occur, reduced nitrogen inputs are expected, and soil and plant nitrogen levels may remain lower (Evans and Belnap 1999).

4.3.8 *Surface Albedo*

Restoration of normal surface albedos and temperatures will depend on the restoration of pre-disturbance cover of cyanobacteria, lichens, and mosses. While cyanobacteria do form a darkish matrix in which other components are embedded, mosses and lichens are much darker and can contribute 40% or more of the cover in an undisturbed crust (Belnap 1993). Consequently, surface albedo recovery will be controlled by factors that control lichen and moss recovery.